SELECTION FOR ENDOSPERM TYPE, MATURITY, AND PLANT HEIGHT IN TWO MAIZE COMPOSITES

BY

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In Malawi farmers store their maize on the cob in cribs made of bamboo strips which are not insect proof. Consequently, there is a considerable quantity of maize grain that is lost due to insect (especially weevil) infestation. Local maize varieties have hard endosperm that makes them more resistant to weevil damage, but these varieties are low in yield and should be replaced. The purpose of this study was to determine the response to phenotypic selection of three traits, namely endosperm type (flint, semi-flint or dent), maturity, and plant height. Data for these traits were recorded on over 1000 plants in each of two populations, Chitedze Composite A (CCA) and Chitedze Composite C (CCC), and each plant was self-pollinated. Groups of 20 of these plants were selected for short and tall height, early and late maturity, and flint, semi-flint, and dent endosperm type. Intercrosses within groups of self-pollinated plants (S_1 lines) resulted in 12 synthetics in each population. These synthetics, along with the original populations, were grown at two locations in Malawi during the 1984/1985 and 1985/1986 seasons. A randomized complete block design was used with five replications at

each location. Data were taken for grain yield, days to silking, plant height, and endosperm type.

There were significant ($P \leq 0.01$) differences among synthetics for traits that were subjected to selection in both populations, indicating that selection on an individual plant basis was effective.

There was a highly significant direct response to selection for the three traits. In addition, selection for plant height had a significant ($P \leq 0.01$) effect on days to silking and endosperm type but not on grain yield.

Heritability estimates by regression analysis and realized heritability values were in the 36 to 50% range with good agreement between the methods.

Correlation analyses showed no relationship between endosperm type and yield in CCA; in CCC there was a positive but small ($r = 0.22^{**}$) correlation between yield and softer kernels. Yield was positively correlated with height and days to silking. There was a low but significant ($P \leq 0.01$) correlation between lodging and plant height in CCA but not in CCC ($r = 0.045$). Lodging was associated with later silking in both populations ($r = 0.67^{**}$ in CCA and 0.40^{**} in CCC).

These results indicate that the CCA and CCC populations can be improved by phenotypic selection for shorter plants, earlier maturity, and flinty kernels. It is suggested that index selection be used, in order to minimize the undesirable correlated responses that might occur if only one trait were emphasized.

INTRODUCTION

Endosperm hardness in maize may be an important trait depending on what the grain is used for. For maize that is marketed for export, physical damage to the grain tends to increase with further handling (Johnson and Russell, 1982). Hill et al. (1949) reported three case studies in which maize lots for export changed as much as four grades before the final destination, even though screenings were removed at several points in route. The more floury-kernel (deeply dented) types tended to break more readily than did the hard-kernel (flinty) types. Also the larger-sized kernels tended to be more susceptible to breakage (Johnson and Russell, 1982).

In Malawi, the processing of the maize grain into flour involves removal of the pericarp, soaking of the grain for several days after the pericarp is removed, and grinding the grain into flour. The process of removing the pericarp may be done manually, as with a mortar and pestle, for example, or by hammermill. The removal of the pericarp, whether manually or by hammermill, causes breakage of the kernels. Large, dented kernels tend to break more than small, roundish, flinty types. As a result, more flour yield is obtained by manual processing with flinty-kernel types than the dented types. Local maize cultivars are mostly of the flinty-kernel types and this has made it difficult for farmers to accept new, higher yielding varieties which are mostly dent types.

Another advantage, for Malawi, of the flinty types is their resistance to pests, especially weevils, during storage. Farmers store their maize on the cob in cribs made of bamboo strips which are not insect proof. Although some farmers use insecticides on their stored maize, the majority do not because of cost of the insecticides.

Local maize varieties in Malawi have acceptable flinty endosperm and processing characteristics, but are undesirable because of low grain yield, excessive height, and susceptibility to lodging. There is, therefore, an urgent need for development of improved varieties which have better grain yield, lodging resistance, and shorter plants along with flinty endosperm.

The objective of this study was to determine the effectiveness of phenotypic selection for three phenotypic traits, flinty-type endosperm, maturity, and plant height in two genetically diverse maize populations.

LITERATURE REVIEW

Starch Molecules and the Genes Affecting Their Development

Many studies have been conducted on the type and quantity of carbohydrates in maize kernels. Much of the early work involved open-pollinated cultivars and was concerned with change in sugar content during development. Post-harvest transformations in sweet corn kernels were also investigated extensively because of their significance in the palatability of the processed product (Alexander and Creech, 1976). Culpepper and Magoon (1924) found that amount of sugars in sweet corn increased up to 15 days after pollination and then decreased slowly during the latter stages of kernel development. Reducing sugars were highest at the initial stages and decreased throughout growth and development. They also observed that sucrose increased rapidly until the 15th day and then decreased slowly during the next 15 days. In this case, most of the sugar was sucrose. Polysaccharides increased continuously during the development of the ear. Sweet corn cultivars, unlike standard dent maize, were high in water soluble polysaccharides.

Brown et al. (1971) studied maize starch granules in endosperms of 24 genotypes during kernel development at 12, 18 and 24 days post pollination. At 12 days after pollination they observed that mutant genotypes were essentially spherical and could not be distinguished in size and shape from normal maize starch. Apparently, morphological differentiation was just beginning at this stage in granule ontogeny

as some mutant genotypes that could not be distinguished from normal could be distinguished from each other. However, the crystalline organization of the mutant and normal starch granules at 12 days post-pollination appeared to be similar. They also found evidence of mutant genes that modify granule properties over the period of 12 to 24 days post-pollination, except su_1, whose granules increased very little in size over the 12-day period. Granule development from a point of similar size at 12 days to differences of size and shape at 18 and 24 days post pollination was dependent on the genotype. In general, most mutant starch granules were smaller than normal at 18 and 24 days; whereas, irregularly shaped granules were exhibited by the genes $aesu_1$ and $dusu_2$ at 24 days post-pollination. They observed that the gene su_2, alone or with du and su_1, reduced the degree of molecular association below that found in normal. The gene su_2 was probably responsible for the development of many molecules that were unable to arrange themselves into crystalline micelles. The authors concluded that variation in the crystalline make-up of the starch granules of ae and su_2 was evident. However, the nature of the variation required additional investigation.

Many mutations in maize affect endosperm components. Several alter the type and quantity of carbohydrates, including starch (Alexander and Creech, 1976). Waxy corn was first reported by Collins (1909). He observed that the waxy mutant was different from normal maize in sugar and starch content. Weatherwax (1922) demonstrated by iodine staining that starch in the endosperm consisted solely of a "rare" form of carbohydrate called "erythrodextrin", currently known as amylopectin. This starch stained red with iodine, in contrast to

"amylodextrin", currently termed amylose, which stained blue with iodine. Bates et al. (1943) and Sprague et al. (1943) confirmed that the waxy endosperm of maize contains starch consisting of nearly all amylopectin, a branched-chain polysaccharide. Bear (1944) had reported three additional waxy mutations in inbred lines of dent maize. Staining reaction and chemical analysis indicated that these three mutations were indistinguishable from the wx allele reported by Collins. Bear's report was primarily concerned with a study of the effects of the wx^a allele on the properties of the endosperm starch. Andes and Bascialli (1941), cited by Brimhall et al. (1945), reported two waxy mutations in the Argentine varieties Colorado Fortin Refugio and Amarillo Fortin Refugio. These were tentatively designated as wx38a and wx38b and shown not to be identical with the Chinese wx type. Andres (1944), cited by Brimhall et al. (1945), reported that these two mutations were similar and had assigned to them the symbol wxA.

It is now generally accepted that the starch granule is usually a mixture of two polysaccharides (Greenwood, 1956; Whelan, 1961). Amylopectin is the major component in most starches, ranging from 75 to 85%, and is of high molecular weight in a magnitude of 1×10^7 micrograms. Amylopectin consists of chains of α-D-(1-4) and α-D-(1-6)-glucosidic linkages which form a branched molecule. Amylose, on the other hand, is primarily linear with α-D-(1-4)-linked glucose residues.

Two sugary genes, designated sugary-1 (su_1) and sugary-2(su_2), were described by East and Hayes (1911) and Eyster (1934). Mangelsdorf (1947) reported two gene mutations, designated dull (du)

and amylaceous sugary (su_{am}), that also altered the carbohydrate properties of maize endosperm. Amylaceous sugary was later found to be allelic to the su_1 gene. Andrew et al. (1944) reported that the recessive allele wx increased sugars and water soluble polysaccharides in either su_1 or Su_1 backgrounds. Cameron (1947) studied the 16 possible endosperm genotypes involving $su_{am}su$ and Du du in an isogenic background. The su_{am} and Du alleles increased total starch and decreased sugars and water-soluble polysaccharides, with the first dose of either allele being the most effective. A similar inverse relationship was found between total starch and percent amylose in the starch. His supersugary genotype, homozygous for sudu, contained only 19% starch. It had 65% amylose with su interacting strongly with du to produce this high value, while that homozygous for su_{am} Du had 81% starch of which only 31% was amylose.

Kramer and Whistler (1949) established that the su_2 gene increased the amylose content to about 35%. Dvonch et al. (1951) showed that the su gene, alone or in combination with wx, su_2, or du, increased water-soluble polysaccharides to over 30% and reduced starch to less than 30%. The gene su_2 did not interact with su or du, but produced a similar increase in amylose regardless of the gene with which it was combined.

Vineyard and Bear (1952) described a gene mutation, termed amylose extender ae, that substantially increased amylose content without drastically decreasing the total starch content. Endosperm starch of ae stocks, in many backgrounds, contains approximately 60% amylose. Deatherage et al. (1954) reported the development of an ae hybrid that was high in starch yield but 60% of the starch was

amylose. Kramer et al. (1958), using various combinations of the genes ae, du, su_1su_2, and wx, found that the amylose contents ranged from zero to over 70%.

Zuber et al. (1960) suggested that the range in amylose content of 54 to 71% in maize inbred lines possessing the ae gene was due to modifier genes. They also reported that starch content decreased as amylose content increased. The development of high-amylose hybrids currently involves the elaboration of ae lines carrying modifier complexes conducive to high-amylose synthesis in hybrid combinations. Cyclical breeding systems have been initiated at the Missouri Agricultural Experiment Station to accumulate favorable major genes (Zuber et al., 1960). A reservoir of genes with additive effects is assumed to be necessary for effective selection. The constitution of double-cross hybrids, with respect to individual inbred lines, would affect the kinds of gene action inherent in the inbreds chosen. The relative importance of additive to non-additive gene action would have considerable bearing on general utility of a given inbred versus its more restricted utility as a parent where the favorable effects were specific for only certain hybrid combinations.

Bear et al. (1958) used the term "amylomaise" as a generic term to describe maize with amylose content above 50% which would be agronomically adapted to commercial production. They suggested the following breeding procedure.

Step 1. Incorporate high amylose factors into inbred backgrounds. This can be accomplished by backcrossing high amylose source genes such as ae, su_2, and du with a series of regionally adapted dent inbred lines. These crosses

would then be selfed twice and high amylose selections would be made within each genotype involved in each inbred germplasm background. This cycle should be repeated through a minimum of three backcrosses.

Step 2. Combine two, three, or more basic amylose-producing genes which have a common recurrent inbred background. Crosses among the appropriate types would be made. It is suggested that such multiple combinations then be self-pollinated and selected ear-to-row through at least two amylose selections. Data at present indicate that it will not be necessary or particularly desirable that the resultant high-amylose inbreds should contain all basic amylose genes in a homozygous condition.

Step 3. Combine the selected high-amylose inbreds into single crosses. Single-cross tests would then be made in order to determine agronomic characteristics and resultant amylose contents. From such data predictions could be formulated for double-cross hybrid production.

The authors concluded that variations in the technique outlined above would be necessary and desirable as more information became available on high-amylose-producing gene combinations and as more actual breeding experience was gained.

Garwood and Creech (1972) studied multiple combinations of gene mutations affecting kernel properties of field maize and sweet corn. They observed the following genes affecting the endosperm: amylose-extender (ae), brittle-1 (bt_1), brittle-2 (bt_2), dull (du), floury-1 (fl_1), horny (h), opaque-2 (O_2), shrunken-1 (sh_1), shrunken-2

(sh_2), sugary-1 (su_1), sugary-2 (su_2), and waxy (wx). They used the standard allele for each gene.

These mutations were studied in the following backgrounds: dent inbreds W64A and W23, sweetcorn inbreds S3-61, 1453, and 15125, and derivatives from the dent single cross W23 x L317. Single and double recessive genotypes of ae, du, o_2, su_1, su_2 and wx were observed in the dent inbreds W64A and W23 after two to four generations of backcrossing. In addition, all single, double, and triple recessive genotypes used in this investigation were observed in a genetic background related to the dent single cross WS23 x L317. All possible combinations of ae, du, su_1, and wx were also examined following five to seven backcrosses to the sweet corn inbreds S3-61, 1453, and 15125.

They observed that the brittle-1, brittle-2, and shrunken-2 mutations resulted in shrunken (collapsed) kernels similar to shrunken-1 in all combinations. The floury-1, horny, and opaque-2 mutants were opaque and were difficult to distinguish. Most of the interactions resulting in new genotypes involved combinations of amylose-extender, dull, sugary-1, sugary-2, and waxy, suggesting biochemical interactions of the products of these genes. The various kernel phenotypes observed were described by the authors as follows: 'etched' indicates a minute wrinkling on the kernel surface; semi-full, semi-collapsed, collapsed, wrinkled, and shrunken describe progressively decreasing kernel size and increasing degree of collapsibility (shrunken kernels contain very little dry matter in the endosperm); opaque, tarnished (caramel-like), translucent, and glassy refer to the texture of the kernel and also describe the endosperm's

ability to transmit light. The authors concluded that knowledge of the various interactions would permit efficient development of multiple gene combinations.

Nature of Endosperm and Yield

A study was conducted by Grogan and Francis (1971) to investigate the influence of single-recessive endosperm mutants on yield and dry matter determination in maize. Seed stocks of the recessive endosperm mutants su_1, fl_1, and O_2 were each crossed with several inbred lines of maize. The F_1 plants were self-pollinated to produce ears segregating for normal and mutant kernels. Careful examination of ears from F_2 plants allowed harvest of samples from homozygous normal, heterozygous, and homozygous mutant plants. The authors observed that the heterozygotes were superior in grain yield to either homozygote, and the homozygous normal yielded more than the mutant in su_1 and O_2 crosses. Husk dry weights were lowest in normal homozygotes of su_1 and O_2, and in the homozygous recessive of fl_2. Leaf and stem dry weights showed inconsistent patterns. Plants from normal kernels had a lower ear, husk, and leaf moisture than those of the homozygous recessive. The harvest index (ear weight/total plant weight) was greater in homozygous normal and heterozygous plants of su_1 and O_2 maize. The heterozygotes studied appeared to have a more totally efficient system for the conversion of light into dry matter.

Brunson and Quackenbush (1962), Curtis et al. (1956), Grogan et al. (1963), and Richey and Dawson (1948) reported reciprocal differences in chemical composition of maize endosperm tissue, other than amylose, in a number of instances. Reciprocal differences in amylose content have been reported previously by Brimhall et al.

(1945), Dunn et al. (1953), Kramer and Whistler (1949) and Vineyard et al. (1958), but reliable estimates of the magnitudes of such effects and tests of their significance were lacking. The evaluation of reciprocal effects is useful in the investigation of the nature of gene action in tissue which is exclusively triploid. An indication of the relative importance of maternal effects, which were confounded with genotypic effects, would be desirable since discrepancies from an additive model are not necessarily relegated exclusively to dominance or epistatic effects (Loesch and Zuber, 1965).

Endosperm Type and Grain Quality

Johnson and Russell (1982) reported that physical damage to maize grain had increased because of field shelling at high grain moisture, high-temperature drying, and high-speed handling equipment. Physically damaged maize tends to break more with further handling, and this is particularly serious for maize that is marketed for export. Hill et al. (1949) reported three case studies in which maize lots changed as much as four grades before the final destination, even though screenings were removed at several points in route, due to increased amounts of broken kernels and foreign material. The foreign buyer compensates for potential grade changes with a discount on the bid, which is passed back to the farmer-producer by discounts at the elevator.

Agricultural engineers have designed improved handling machinery to reduce physical damage; however, genetic modification of the maize kernel is another approach to reducing physical damage. This approach has received little attention because the genetics of physical grain-quality traits are not well known (Johnson and Russell, 1982).

Duncan et al. (1972) and Jennings (1974) observed differences among several widely grown single-cross hybrids for visible damage, percentage foreign matter, test weight, and breakage with the Stein tester method. The use of certain inbred parents promoted poor grain quality in hybrids, and these authors suggested that selection of parental lines might contribute quality to single-cross hybrids. Significant differences among hybrids, testers, and lines for Stein breakage were observed for widely grown Corn Belt hybrids (Russell, unpublished data cited by Johnson and Russell, 1982).

In their investigations, Johnson and Russell also observed that the more floury-kernel (deeply dented) types tended to break more than did the hard-kernel (flinty) types. The larger-sized kernels tended to be more susceptible to breakage. The authors concluded that except for specific gravity, progress could be made with selection for any of the traits, based on variance components and heritability estimates. Selection for visual ratings of endosperm type (e.g. flint, dent, etc.) was particularly appealing as a screening device because the data could be taken rapidly and in the field. There is some concern that selection for the hard starch (flinty) type might mean selection for small seed (e.g. popcorn as an extreme) and eventually lower yield (Russell and Machado, 1978). Correlation results showed no relationship between endosperm type and seed size or weight.

Recurrent Selection

Population improvement in maize is now being carried on by many breeders, who use a system generally called recurrent selection (RS). The improvement results from accumulation of favorable genes during recurring cycles. Simple RS is performed by selecting superior plants

and making many intercrosses among selected plants or their progenies, and is most useful for characters having high heritability. Recurrent selection for general combining ability (GCA) (Jenkins, 1940) and specific combining ability (SCA) (Hull, 1945) employ test cross evaluation using broad and narrow base testers, respectively. Reciprocal recurrent selection (RRS) (Comstock et al., 1949) uses two heterozygous populations, each being the tester for lines from the other, simultaneously.

A breeding method similar to RS for GCA was first suggested by Hayes and Garber (1919). They outlined a procedure for developing a synthetic population with high protein content by selfing, selecting, and subsequent crossing. However, this method was not adopted at that time. Later, after Jenkins (1940) presented the first detailed description of the methodology for GCA, many breeders have stressed the importance of a broad base tester since it has been considered superior to narrow base testers for identification of lines which provide greater average performance in combination with other lines.

Hull (1945) first proposed RS for SCA, and suggested the use of a homozygous line as a tester. He believed that overdominance was the major type of gene action present in adapted varieties, since additive gene action was presumably exhausted by previous selection. Comstock et al. (1949) proposed and outlined a method for RRS which was considered to be effective regardless of level of dominance present, but it would have maximum efficiency if overdominance or dominance by dominance interaction was present in the populations used. Current theory further suggests that RRS is appropriate whether additive or nonadditive gene action is predominantly present.

The considerable time and progeny testing needed to extract superior homozygous lines encouraged the need for early testing, which essentially helped RS to develop. Jenkins (1935) studied topcross yield results, using lines which represented eight generations of selfing and discarded lines of each generation, and concluded that inbred lines that showed superiority in the early generations of selfing remained relatively stable. Lonnquist (1950) presented conclusive evidence that continued selection and testing after the S_1 generation would be most profitable for those lines exhibiting highest top cross performance in early generations.

Gene Action

Partitioning of genetic components of variance based on type of gene action for various mating designs has provided a scale for measuring the inheritance of agronomically useful characters. Robinson et al. (1949) and Gardner et al. (1953) estimated gene action for yield in the overdominance range. However, later studies by these workers showed that these estimates of overdominance were due to linkage disequilibrium. Thompson et al. (1971) showed that additive and dominance parameters were responsible for an average of 90% of the variability in the inheritance of ear height.

Half-Sib Method and Effectiveness of Testers

The half-sib progeny test, where selected progenies are mated among themselves, uses one-fourth of the additive genetic variance and requires two generations per cycle of selection. Where the selected selfed male or female parents are mated among themselves, it utilizes one-half the additive variance and requires at least three generations per cycle. Improvement by this method depends not only on the genetic

constitution of the population but also on the type of tester used. Rawlings and Thompson (1962) crossed six lines classified as high, intermediate, and low yielding to high- and low-yielding testers and found that a low-yielding tester would discriminate more effectively among combining abilities of lines crossed with it than would a high-yielding tester. In their theoretical comparison, they showed that when a tester is homozygous recessive at all loci, the genetic variance among testcross progenies is larger and it has an increasing advantage as dominance increases, compared with heterozygous testers. Allison and Curnow (1966), from a mathematical approach of the two-allele locus, stated that if partial to complete dominance is of primary importance, a low-yielding population selected from the parental variety would be the best tester. Lonnquist (1968) showed that the highest yield resulted from the intercrosses of lines selected on the basis of performance with the parental population. Selection on the basis of an unrelated tester resulted in slightly better yield when selected high-by-low groups were crossed than when high-by-high groups were crossed. This result suggests that the parental tester emphasizes additive gene action while the unrelated tester emphasizes dominance gene action.

Selection for GCA, which is primarily a function of additive gene action, has historically used broad-base testers while selection for SCA, which is primarily a function of nonadditive gene action, used a narrow-base tester. However, recent results show that narrow-base testers also improve GCA, perhaps even more effectively than broad-base testers. Russell et al. (1973) evaluated populations developed from five cycles of recurrent selection for combining ability for

yield with the inbred tester B14 in two populations, 'Alph' and the F_2 of (WF9 x B7), in crosses with the original tester (B14) and with an unrelated population, BSBB. The crosses with B14 indicated an average yield increase of about 0.31 Mg ha^{-1} per cycle in Alph and about 0.13 Mg ha^{-1} per cycle in (WF9 x B7) and those with BSBB about 0.36 Mg ha^{-1} per cycle in Alph and about 0.15 Mg ha^{-1} per cycle in (WF9 x B7). These results show that GCA as well as SCA were improved by use of the narrow-base tester. Horner et al. (1973) completed five cycles of RS, using an inbred line and the parental population as testers and S_2 progeny performance per se, in three parallel programs. The 15 populations produced by these methods were evaluated for average combining ability with the parental population and an unrelated broad-base tester. They obtained a 4.4% yield gain per cycle from the Inbred Tester Method compared with 2.4 and 2.0% from the Parental Tester and S_2 Progeny Methods, respectively. They indicated that the inbred tester was evidently homozygous recessive at many important loci which would result in more successful selection for dominant favorable alleles than would use of a broadbase, heterozygous tester. Walejko and Russell (1977) evaluated the progress of RS in which the inbred Hy was the tester for two open pollinated varieties and indicated that the yield gain observed for the Hy testcrosses and the population crosses were expressed equally well in testcrosses with unrelated testers.

The significance of these findings [Russell et al. (1973), Horner et al. (1973), and Walejko and Russell (1977)] is that (a) inbred testers are very effective for improving the GCA of a population and

(b) the fear that narrow-base testers improve only SCA in selected populations was unfounded.

The earliest report on the effectiveness of RRS was made by Douglas et al. (1961). They compared performances of first, second, and third cycle composites of each variety and crosses among them and concluded that selection was slightly effective in accumulating favorable alleles in the first two cycles of 'Ferguson's Yellow Dent' and only in the first cycle of 'Yellow Surecropper.' Average combining ability of the varieties was improved only in the first cycle of selection. Eberhart et al. (1973) evaluated the progress from five cycles of RRS in varieties BSSS and BSCB1 and obtained a linear improvement of 0.27 Mg ha^{-1} (4.6%) per cycle from BSSS $(R)_n$ x BSCB1 $(R)C_n$ population crosses. However, there was no significant change in the parents themselves.

Selection Based on Selfed Progeny Performance

Selfing is the major type of mating that changes the genotypic frequency of a formerly random-breeding population. Selfing rapidly reduces a population to homozygosity regardless of the number of heterozygous loci initially present. Let us suppose that randomly selfed S_0 plants were heterozygous (Aa) for all loci. In the first generation, S_1 progenies will be 50% homozygous (AA and aa) and 50% Aa. S_2 progenies of randomly selfed S_1 plants will be 75% AA and aa and 25% Aa. If the AA and aa genotypes together in the S_0 generation are assumed to be at the same proportion as the Aa genotype, then randomly selfed S_0 plants will produce S_1 progenies with 75% AA and aa and 25% Aa and likewise S_1 plants will produce S_2 progenies with 87.5% AA and aa and 12.5% Aa. The gene frequency of S_2 lines will be the

same as in the S_0 plants, but the genotypic frequencies will vary depending on the gene frequency of the initial population.

When S_2 progeny means are compared,

AA will be better than Aa for $\underline{d} < 1.0$,

AA will be equal to Aa for $\underline{d} = 1.0$,

Aa will be greater than AA for $\underline{d} > 1.0$,

where $\underline{d}$ is a measure of dominance, $\underline{d} \geq 0.0$. This means that if dominance is less than complete, selection will favor AA genotypes; if dominance is complete, selection will favor both AA and Aa; and if there is overdominance ($\underline{d} > 1.0$), selection will favor Aa alone. With selfing, however, the frequency of Aa genotypes is low.

Examination of inbreeding and its effects on genetic variation among the selfed progenies is very helpful for understanding the changes that would occur with selfing. Maximum inbreeding is obtained when like gametes unite, A with A or a with a; under such conditions, the inbreeding coefficient (F) will be one because the gene controlling a particular character is fixed. A random mating population, on the other hand, has an F value of zero. If a base population with gene frequency $p = q = 0.5$ is selfed, F values for each generation will be $S_0 = 0.00$, $S_1 = 0.50$, $S_2 = 0.75$, and $S_\infty = 1.00$.

The equation for F with selfing as given by Falconer (1960) is $F = \frac{1}{2}(1 + F_p)$ where F_p is the inbreeding coefficient of the parent.

The increase in the F value is inversely related to the decrease of the frequency of heterozygotes in a selfed series.

Horner et al. (1969) showed the fractions of the genetic variance among selfed progeny means that are due to additive and dominance gene effects to be

$$2pq\ (1 + F)\left[a + \tfrac{1}{2}d\ (q - p)\ \frac{(1 - F)}{(1 + F)}\right]^2 \text{ and}$$

$$pq\ (p + Fq)\ (q + F_p)\ \frac{(1 - F)}{(1 + F)}\ d^2, \text{ respectively,}$$

where F is the inbreeding coefficient of the parental plant and the rest are the same as before. They used $\frac{1}{2}d$ instead of d for the Aa genoptype since they were interested in the progeny means rather than individual plants. They stated that the variance among selfed progeny means that is due to additive gene effects is large compared with that due to dominance effects. As the generation of selfing increases, the frequency of heterozygotes decreases and the fraction of the genotypic variance that is due to dominance decreases regardless of the level of d.

Selection Based on Testcross Performance

Selection based on testcross performance largely depends on the amount of variance among testcross means. Horner et al. (1969) used the following formula, similar to that of Rawlings and Thompson (1962), to estimate the genetic variance in a two-allele system.

$$V = 0.5\ pq\ (1 + F)\ [a + d\ (Q - P)]^2,$$

where P and Q are frequencies of A and a, respectively in the tester and the other symbols are the same as before. They stated that if S_0 plants or S_1 lines are tested, F = 0.0. If S_1 plants, which are equivalent to S_2 lines, are tested, F = 0.5. In the absence of epistasis, the total variance is the sum over all loci. The expression shows that the variance of testcross means is a function of the additive effect of a gene or the average effect of a gene substitution [a + d (Q - P)], gene frequency in both the tested and the tester populations, and inbreeding of the tested plants. If a further assumption is made that A is also the favorable allele over a in the tester, the theoretical effectiveness of a tester can be visualized.

1. When d = 0, selection for high performance of the individuals of the population being tested will not be influenced by gene frequency in the tester, because d(Q - P) = 0 in the expression.
2. When $\underline{d} < 1.0$, selection for high performance of the individuals of the population being tested favors AA genotypes. If the population being tested has a low frequency of AA genotypes, the rate of improvement will be larger than when P is large.
3. When $\underline{d} = 1.0$, selection for high performance is ineffective if P = 1.0, because, in such circumstances, selection by testcross performance will not discriminate between individuals of the population tested, since AA = Aa. However, as the frequency of P gets smaller, more individuals with aa genotypes will be discarded, because

a gametes of the tester are more likely to unite with a of the population tested.

4. When $\underline{d} > 1.0$ and P = 1.0 in the tester, selection will favor aa genotypes in the population being tested.

Aa genotypes will also be selected but less frequently, because gametes from Aa genotypes can unite with the tester gamete. AA genotypes, however, will be discarded. As P decreases, selection for AA individuals increases and at P = 0.5 the frequency of selecting each genotype will be the same since either A or a gametes of the tester will only show overdominance when united with a and A gametes of the population tested, respectively.

Horner et al. (1969) presented a very descriptive figure showing a comparison of the expected genotypic variances that are due to additive effects for selfed progenies and for testcross progenies based on the expressions shown for selfing and testcross progeny methods. In this model, the parental population was used as a tester. Their figure showed that the expected additive variance among the selfed progenies is much larger than among testcross progenies. Up to p = 0.2, the expected variance is similar for S_1 and S_2 progenies, but very low for testcross progenies. At $p > 0.2$, S_2 progenies show the greatest variation and testcross progenies the least variation. At p = 0.7, variance among S_2 progeny means would be 14 times larger than among testcross progenies, and variance among S_1 progeny means would be about four times larger than testcross progenies at p = 0.5. This shows that S_2 progenies provide more opportunity for selection than

either S_1 and testcross progenies while testcross progenies provide the least opportunity.

Reciprocal Recurrent Selection

Reciprocal recurrent selection has proven to be an effective method for improving two populations for combining ability with each other simultaneously at all levels of dominance. It was designed for characters that exhibit low heritabilities and high heterosis. Comstock et al. (1949), who proposed the method, compared theoretical limits of improvement using RS for SCA and GCA, and RRS and concluded that

1. When $\underline{d} < 1.0$, the improvement limit is the same for RS for GCA and RRS, but lower for SCA. The superiority of Aa genotype declines as the value of $\underline{d}$ is reduced, and so RS for SCA will be less effective.
2. When $d = 1.0$, RS for GCA, SCA, and RRS will be equally effective. If the broad-base tester is homozygous dominant for many favorable alleles, selection for GCA will be less efficient, because all testcross genotypes would have the same value.
3. When $d > 1.0$, RS for SCA and RRS will be the same but RS for GCA will be inferior to both methods, because the mean of the individuals selected on the base of performance with the broad-base tester is the average of all genotypes, which would result in low response relative to the other two methods.

Cress (1966) compared RRS with within-population selection (WPS) based on theoretical considerations. Methods by which WPS can be

accomplished include RS for GCA and full-sib selection in two populations, x and y. The rate of progress was measured by

$$C = {}_{xy}M_{yx} - \tfrac{1}{2}({}_{xx}M_{xx} + {}_{yy}M_{yy}),$$

where C is the difference which is the comparison of the rate of improvement between RRS and WPS,

${}_{xy}M_{yx}$ is the mating system for RRS, and

${}_{xx}M_{xx}$ and ${}_{yy}M_{yy}$ are mating systems within populations X and Y, respectively.

If A is the favorable gene over its allele, a, in both populations, and p and P are the gene frequencies for the favorable allele in the X and Y populations, respectively, the theoretical rate of improvement is:

1. When $(p + P) < 1.0$, RRS is better than WPS for all positive dominance.
2. When $(p + P) > 1.0$, WPS is faster in the rate of improvement than RRS for levels of dominance including complete dominance because the larger proportion of the favorable alleles contributes larger additive variance with the WPS method.
3. If overdominance is present, RRS is better when $(p + P)$ 1.0 and the difference between p and P must be large enough to see a pronounced result. If p = P, RRS = WPS, and the rate of progress in RRS is dependent on the additive variance in the testcrosses.

Cress (1967), using a simulation method, also compared RRS as proposed by Comstock et al. (1949), RRS_s, modified by an additional selfing generation prior to testcrossing, and RRS_c, using the original parents as testers over 30 cycles. Generally, the results showed that RRS and RRS_s methods provided high and linear mean response in hybrid combinations between populations at all levels of dominance, with RRS_s being superior over RRS in the rate of progress in early cycles.

Comparisons of S_1, S_2, and Half-Sib Methods

Selfed and half-sib progeny selection methods have been compared more frequently since the early 1960s, but the question as to which method is most effective still remains unanswered. The first attempt was made by Davis (1934) in which he compared selfed lines and their crosses with an unrelated open-pollinated variety tester. He indicated that average yield of the first and second inbred generations was important for selection. Genter and Alexander (1962) made a comparative performance test between S_1 progenies and progenies selected on the basis of testcross performance with single cross testers. They found more variation among means and less environmental effect from S_1 progenies than from testcrosses. Lonnquist and Lindsey (1964) and Lonnquist and Castro (1967) made similar reports that the S_1 progeny method was more effective for selection than testcross methods with related and unrelated testers. Duclos and Crane (1968), however, found no significant difference between S_1 progeny and testcross methods.

Comparisons of advanced populations developed by different methods of recurrent selection have been made in order to evaluate the effectiveness of the methods. Genter (1966) found mean yield

increases of 31% and 18% with two cycles of S_1 and testcross selection, respectively. In 1973, he obtained a population yield of 0.9 Mg ha^{-1} (11%) more from the second cycle of S_1 selection than from the testcross populations. However, Genter and Eberhart (1974) obtained the same yield response from both VCBS(S)C_4 and VCBS(HT)C_3 developed from Virginia Corn Belt-Southern Synthetic by four cycles of RS for S_1 progeny yield and by three cycles of half-sib selection, respectively. BSK(S)C_4, developed from Krug Hi syn-1 by four cycles of S_1 selection, and BSSS(HT)C_7, developed from 'Stiff Stalk Synthetic' by seven cycles of half-sib selection, failed to show any improvement. Carangal et al. (1971) indicated that S_1 progeny evaluation was more efficient than testcross evaluation even for GCA. Burton et al. (1971), using a double cross tester for four cycles, obtained about a 6% yield increase from the testcross series, but 16% from the selfing series for yield of populations per se. Combining ability with four testers was also improved more by the S_1 method.

Horner (1963) compared S_1 lines and S_1 plants (which are equivalent to S_2 lines) and stated that selection for combining ability can be done more effectively among individual S_1 plants than among S_0 plants or S_1 lines. The variance component estimate for crosses involving S_1 plants was larger than for crosses of S_1 lines. This shows that subsequent selfings do provide an opportunity for more effective selection. Horner et al. (1969) found that the S_2 progeny method was as effective as the parental tester method for population improvement and suggested that it places more emphasis on contribution of homozygous loci than heterozygous loci, whereas the parental tester method emphasizes the contribution of heterozygous loci to a greater

extent, resulting in a higher yielding syn-3 population. In 1973, from two additional cycles, they reported a gain in GCA of 4.4% per cycle from an inbred tester method compared with 2.4% and 2% for the parental and S_2 progeny methods, respectively.

Regardless of the type of gene action involved, RRS is, theoretically, considered effective in producing lines with improved SCA for yield and vigor between two populations. Thomas and Grissom (1961) evaluated RRS for popping volume, grain yield, and resistance to root lodging in popcorn and concluded that RRS was effective in improving the mean of the two populations simultaneously. However, nearly the same improvements were made when S_4 lines were developed from direct selfing in the two populations. Moll and Stuber (1971) compared full-sib family selection and RRS for higher grain yield in the varieties Jarvis and Indian Chief following six cycles of selection, and stated that heterosis in the variety hybrid increased about 30% more after RRS than after full-sib family selection within each population.

Darrah et al. (1972) obtained an 0.8 Mg ha^{-1} larger gain in yield from RRS compared with the modified ear-to-row method in variety H611, but there was no significant difference between methods in varieties KII and Ec 573. Russell and Eberhart (1975) evaluated three crosses among the BSCB (R) C_5, BSSS(R)C_5, and BSSS(HT)C_6 populations improved by five cycles of RRS and six cycles of testcross selection with a double- cross tester other than a tester from the population crosses. There was no significant difference in grain yield among the population crosses. Robinson (1976) obtained a higher estimate of genetic variance from S_2 line evaluation than from half-sib progeny

evaluation in the initial cycle of a selection program comparing the RRS and S_2 progeny methods.

Mass Selection

Williams and Welton (1915) presented data on the effectiveness of mass selection for several ear characters. They concluded that selection was not effective in separating the original population into two distinct groups based on ear length. They also found that there was no important correlation between ear length and yield. They attributed the lack of effectiveness of mass selection to (1) small selection differential, i.e. the average difference in ear length for the two contrasting types (long and short) was 6.3 cm; and (2) lack of parental control because the contrasting selections were grown in adjacent plots to increase the accuracy of yield comparisons. This meant that there was no control of pollination.

Gardner (1961) refined the techniques for mass selection by suggesting a "grid" system (selection of plants within blocks) as a means of reducing the effect of environmental variation. He observed that when selection was practiced on the maternal plants only, gain was reduced because of the lack of parental control for the pollen source. For a trait which is expressed before pollination, undesirable plants can be eliminated to give parental control of both sexes. The author concluded that selecting both sexes would give twice as much gain as selection for one sex only.

Gardner (1968) reported an increase of grain yield of 2.7% per cycle per year in a maize variety known as Hays Golden in a mass selection program. Mathema (1971) reported an average yield increase of 5% per year in semi-exotic maize populations in Nebraska. Prolificacy was also increased by the same percentage.

Hallauer and Sears (1969) did mass selection following Gardner's (1961) "grid" system in the maize varieties Krug (six generations) and Iowa Ideal (five generations). Selection was for grain yield, and usually resulted in an increase in plant and ear height but not in grain quality. The lack of response was probably due to (1) very high plant density, (2) genotype x environment interactions, and (3) use of rectangular instead of square subplots. Similar results were reported by Darrah et al. (1972) in Kenya.

Hallauer and Sears (1972) reported a decrease in the interval from planting to silking by 20 days (3.8 days per year) in the Eto maize variety after 5 cycles of mass selection in Iowa. A correlated response in decreasing plant height of 75 cm was observed. They also observed heritability estimates (broad sense on an individual plant basis) of 59% and 58% for silking date and plant height, respectively.

Seventy generations of selection for protein and oil contents in Illinois (Dudley, 1974) in Burr's white maize variety resulted in means of 12, 8, 27, and 10 standard deviations away from the original mean for high protein, low protein, high oil, and low oil contents, respectively. These changes were obtained by evaluating ears from approximately 6,000 plants over the 70-year period in each of the four populations. In contrast, only 2.6×10^{-12} of the individuals in a normally distributed population are expected to exceed the mean by 7 or more standard deviations.

Arboleda-Rivera and Compton (1974) did mass selection for prolificacy and grain yield in maize in different selection environments, beginning with the same original populations. They used three subpopulations of "Mezcla varieties Amarillos" population of

maize: MVA-A, MVA-B, and MVA-AB. The environment under which selection was done included (1) MVA-A, selected in the rainy season (A); MVA-B, selected in the dry season (B); and MVA-AB, selected in both seasons (AB). Three cycles were undertaken in MV-A and MV-B whereas six cycles were undertaken in MV-AB.

Mass selection in MV-A resulted in an increase in grain yield of 10.5% per cycle when tested in A seasons (direct response) and only 0.8% when tested in B seasons (indirect response). For ears per plant the corresponding responses were 8.8% and 1.0%. The direct response for grain yield in MV-B was only 2.5% per cycle whereas it was 7.6% when tested in A seasons. The gain in ears per plant was 11.4% per cycle. In MV-AB there was a gain in grain yield of 5.3% and 1.1% per cycle in the tests in A and B seasons, respectively. For prolificacy, the respective gains were 7.0% and 3.3% per cycle.

The authors concluded that (1) almost as much gain per year in grain yield could be achieved by selection in the individual season (A or B) as one would achieve by continuous selection (AB), and (2) selection for prolificacy was more successful when performed under weather stress as shown by the MVA-B subpopulation.

The most desirable maize variety for Malawi is one with hard flinty endosperm because of its resistance to storage pests and also its good pounding qualities when it is prepared for food. However, it appears that not much work has been done to make a direct comparison in yield and other agronomic traits between the hard and dent endosperm maize types. This study, therefore, had the following objectives: (1) to determine the effectiveness of visual selection for three phenotypic traits, flint type endosperm, maturity, and plant

height, in two genetically diverse composite maize varieties; (2) to determine the correlation between these three traits and yield; and (3) to determine the effectiveness of selection for these three traits in an environment different from the target environment.

MATERIALS AND METHODS

Materials

The two maize composites, Chitedze Composite A (CCA) and Chitedze Composite C (CCC), were bred at the Chitedze Agricultural Research Station in Malawi. Composite A consisted of 24 entries, most of which were local varieties. Composite C was made from eight exotic entries, seven of which were broad-based populations obtained from the Center for the Improvement of Maize and Wheat (CIMMYT) in Mexico. The entries of the two composites are presented in Table 1.

To develop CCA, 24 varieties selected on the basis of their performance were grown variety-to-row in isolation in the 1967/68 season. This was the beginning of what was known as a "mixing process." The varieties were allowed to random pollinate, and at the end of the season, they were harvested and each variety was kept separately. This mixing process was repeated for three more generations. No selection was done except for discarding rotten ears. During the last two generations of random mating the procedure was modified as follows to hasten the mixing process. A seed bulk of the 24 entries was planted around the plot to provide pollen, and each of the 24 entries was used as female and the plants were detasselled. In the 1970/1971 season, when the fourth generation of mixing was completed, equal quantities of seed (by number) of each of the 24 entires were mixed to form CCA C0 as a bulk population. This

Table 1. Entries used in developing CCA and CCC.

CCA				CCC*
Entry	Origin	Entry	Origin	
LH7	Local	SV41	Local	Across 7425
LH11	"	SV42	"	Cotaxtla 7429
LH20	"	SVK1	"	
Local (unselected)	"	SVK5	"	Across 7422
SV17	"	SVHA1	"	Maracay 7543
SV26	"	H613B	Kenya	Gemeiza 7523/2
SV27	"	KCE	"	
SV28	"	Embu I	"	Obregon 7544
SV29	"	Embu II	"	
SV33	"	E.P. Comp	Zambia	Ilonga 7521
SV37	"	ZCA	"	SR52
SV 40	"	Mexican 'T' lines	Mexico	

*All entries in CCC were from CIMMYT, Mexico, except SR52, a dent hybrid from Zimbabwe.

Table 2. The four variety crosses that were finally composited into CCC.

Across	7425	x	Cotaxtla	7429
Across	7422	x	Maracay	7543
Gemeiza	7523/2	x	Obregon	7544
Ilonga	7521	x	SR 52	

material has been maintained by seed renewal in isolation plots. It has variable endosperm characteristics.

To develop CCC, a process known as chain crossing was used. Seven entries were selected on the basis of their performance world wide in CIMMYT Variety Trials (EVT12 and ELVT 18). These entries consisted of late tropical populations of variable endosperm types (flints and dents). SR 52, a high yielding dent hybrid from Zimbabwe, was included to bring the number of entries to eight. The eight selections were planted in eight rows (one row for each selection). Chain crosses were made in the 1976/1977 season in the following way: row 1 x row 2, row 2 x row 3, -----, row 8 x row 1. The eight crosses were evaluated in replicated trials at four locations in the 1977/1978 season. On the basis of yield and other agronomic characters, the four best crosses were identified (Table 2) and were planted each cross to one row to continue the chain crossing program. Those which performed badly were discarded. Selection was also based on resistance to leaf blight (Helminthosporium turcicum) and rust (Puccinia spp.) because CIMMYT varieties show marked susceptibility to these leaf diseases under Malawi conditions. Two more generations of chain crossing were made followed by one generation of random mating in an isolation plot to produce CCC C0 (the bulk composite) in the 1980/1981 season. It consists of both flint and dent endosperm types, and has been maintained by random pollination in isolation ever since.

Methods

To initiate the present study, 2,000 plants of each of the two maize composites CCA C0 and CCC C0 were randomly selected and tagged in the 1983/1984 season. These were self-pollinated at the Chitedze

Agricultural Research Station to produce S_1 lines. Various measurements such as ear and plant height, lodging, disease assessment, and silking dates were recorded on individual S_0 plants. At harvest, S_0 ears were classified on the basis of endosperm type into flint, semi-flint (intermediate) and dent. A summary of the classificaiton of the plants for days to silking, plant height, and endosperm type is given in Table 3.

In the 1984 dry season, the following combinations of S_1 lines were intercrossed at the Kasinthula Agricultural Research Station under flood irrigation:

CCA: Synthetic No. 1 $M_1H_1G_1$ early short flints
" " 2 $M_1H_1G_2$ early short semi-flints
" " 3 $M_1H_1G_3$ early short dents
" " 4 $M_1H_2G_1$ early tall flints
" " 5 $M_1H_2G_2$ early tall semi-flints
" " 6 $M_1H_2G_3$ early tall dents
" " 7 $M_2H_1G_1$ late short flints
" " 8 $M_2H_1G_2$ late short semi-flints
" " 9 $M_2H_1G_3$ late short dents
" " 10 $M_2H_2G_1$ late tall flints
" " 11 $M_2H_2G_2$ late tall semi-flints
" " 12 $M_2H_2G_3$ late tall dents

CCC: Synthetic No. 1 $M_1H_1G_2$ early short semi-flints
" " 2 $M_1H_1G_3$ early short dents
" " 3 $M_1H_2G_2$ early tall semi-flints
" " 4 $M_1H_2G_3$ early tall dents
" " 5 $M_2H_1G_2$ intermediate short semi-flints

Table 3. Observations made on S_0 plants for three traits in CCA and CCC in the 1983/84 season at Chitedze.

Trait	CCA		CCC	
Silking (days)	Plants observed	%	Plants observed	%
61-66 (early)	5	0.4	243	21.4
67-70 (intermediate)	149	12.4	583	51.3
71-83 (late)	1051	87.2	311	27.4
TOTAL	1205		1137	
Plant height (cm)				
205-250 (short)	15	1.3	263	24.2
251-300 (tall)	277	23.3	750	69.1
301-395 (tall)	898	75.5	72	6.6
TOTAL	1190		1085	
Endosperm type+	Ears observed		Ears observed	
Flint	198	19.1	92	9.1
Semi-flint	455	43.9	409	40.3
Dent	383	37.0	513	50.6
TOTAL	1036		1014	

+Flint: all kernels on the ear were full and hard, with no depressions.
Semi-flint: about 50% of the kernels were flint.
Dent: all kernels had depressions.

" " 6 $M_2H_1G_3$ intermediate short dents

" " 7 $M_2H_2G_2$ intermediate tall semi-flints

" " 8 $M_2H_2G_3$ intermediate tall dents

" " 9 $M_3H_1G_2$ late short semi-flints

" " 10 $M_3H_1G_3$ late short dents

" " 11 $M_3H_2G_2$ late tall semi-flints

" " 12 $M_3H_2G_3$ late tall dents

Procedure for Making Combinations

Each of the 12 combinations in each composite consisted of 20 parental S_0 plants (S_1 lines) of similar maturity, plant height, and endosperm type. The lines in each treatment combination were crossed in pairs reciprocally. Pollen was collected from 10 plants of each line and applied on an equal number of plants of another line. This resulted in 10 ears from each of the 20 lines (200 ears). An equal number of seeds from each ear were bulked to produce a treatment combination. The recombination plots were planted out again at Chitedze in the 1984/1985 season because some of the lines failed at Kasinthula, resulting in an unequal number of lines in each treatment combination. However, the crossing procedure at Chitedze was modified so that 10 lines out of the 20 in each treatment combination were used as males to pollinate the other 10 lines. The procedure of pollen collection was the same as at Kasinthula, i.e. pollen bulks of 10 plants were used on 10 female plants in each line. This means that 10 ears were harvested from each line, and there were 10 lines from each treatment combination (100 ears). Each composite produced 12 treatment combinations (12 synthetics) giving a total of 24 synthetics from two composites. The original populations, CCA CO and CCC CO,

were bulk-sibbed for seed renewal to be included in the experiments as checks. Pollen was collected from 100 plants and bulked prior to applying it on 100 other plants. The total number of entries for each experiment was 13. There were two separate experiments, one of each composite.

Experimental Design

The 12 synthetics of CCA and 12 of CCC described above, together with the two checks, were evaluated in separate experiments in four-row plots at the Chitedze and Chitala Agricultural Research Stations, in Malawi during the 1984/1985 and 1985/1986 seasons. The two center rows constituted the net plot, and the two outer rows were border rows. Chitedze is 1000 m above sea level and receives ample rainfall (more than 1000 mm per annum). Chitala is 100 km east of Chitedze at 600 m above sea level and receives rather low rainfall (less than 500 mm per annum), sometimes not enough to support a maize crop. It is in a very hot marginal area for maize production. Row spacing was 90 cm and the plants were spaced 30 cm apart in the rows. Two seeds were planted per hill and the plants were thinned to one per hill when they reached 15 cm height. Each plot consisted of 80 plants, 40 in the net plots at both locations.

A randomized complete block design was used with five replications at each location. The plots at both locations received 120 kg ha^{-1} of N and 80 kg ha^{-1} P_2O_5. Some pesticides were used at both locations against termites.

Data Collection

Data on total number of plants, ear and plant heights, silking dates, husk score, and lodging were taken in the two center rows of

each plot. Forty tags (one for each plant) were fixed on the plants in every plot to make it easy for record taking. Maturity was recorded on the tag as the date on which silks were first observed on the ear. Later, the number of days from planting to silk emergence was determined for each individual plant and a plot mean was calculated. Ear and plant height measurements were also recorded on the tag for individual plants. Means were later calculated for each plot. Plant height was measured from ground level to the tip of the main tassel branch, whereas ear height was measured from ground level to the node bearing the topmost ear. A husk score for each plot was determined on a one to nine rating scale, one being best with a relatively tight husk and well-covered ears and nine lacking such characteristics. Lodging was also taken on a one to nine rating scale where one was assigned to a plot with less than 10% of the plants lodged and nine with more than 90% of the plants lodged. Lodging in this situation applies to both root and stem lodging. Both leaf blight and leaf rust scores were made on the basis of a one to nine scale, where one was assigned to a plot with less than 10% of the plants infected and nine with more than 90% of the plants infected by each disease.

At harvest, data on number of plants erect, total number of ears, number of ears rotten, and endosperm type were recorded. On endosperm type, a scale of one to five was used on each individual ear. One represented an ear which had 100% flint kernels, and five represented an ear which was completely dent (no flint kernels at all). Each score of one to five was multiplied by the number of ears in that

class in each plot, and the sum of the products was divided by the total number of ears in the plot to obtain a single value, which is the grain index. The reason for working out an index was that more endosperm variation was observed in the bulk trial material than was observed in the S_0 ears which were classified into flint, semi-flint and dent. Grain yield per plot (in kg) was taken by weighing the ears, and taking a sample of 15 ears to shell and determine grain weight and moisture content. Shelling percentage was calculated by dividing grain weight of sample by ear weight of sample per plot and multiplying by 100. To determine weight of grain for each plot, the shelling percentage of each plot was multiplied by the respective total weight of ears. The calculated grain weights were corrected to 12.5% moisture. The second season's yield test was run by different crew because the author had returned to the U.S.

Statistical Procedure

The main interest in this study is in the effects of selection on grain yield, maturity, plant height, and endosperm characteristics. Therefore, analysis of variance (ANOVA) was made for the four traits using the procedure of SAS-76 program for RCBD (Barr et al., 1976). This was a combined analysis of the 13 synthetics of each experiment over two locations and two years of testing.

The basic model is given below:

$$Y_{ijkl} = \mu + L_i + Y_j + (LY)_{ij} + R_{k(ij)} + S_l + (SL)_{il} + (SY)_{jl} + (SLY)_{ijl} + \xi_{ijkl}$$

$$i = 1, 2$$

$$j = 1, 2$$

$k = 1, 2, \ldots\ldots, 5$

$l = 1, 2, \ldots\ldots, 13$

where Y_{ijkl} is the mean response associated with the ith location, jth year, kth replication, and lth synthetic,

μ is the overall mean,

L_i is the effect of the ith location,

Y_j is the effect of the jth year,

$(LY)_{ij}$ is effect of the interaction of the ith location and the jth year,

$R_{k(ij)}$ is the effect of the kth replication nested in the ith location and the jth year,

S_l is the effect of the lth synthetic,

$(SL)_{il}$ is effect of the interaction of the ith location and the lth synthetic,

$(SY)_{jl}$ is effect of the interaction of the jth year and lth synthetic,

$(SLY)_{ijl}$ is effect of the interaction of the ith location, jth year and lth synthetic, and

ξ_{ijkl} is random component of error.

The effects of locations and years were assumed random and the effects of synthetics were assumed fixed, in the above model.

Table 4. Analysis of variance.

Source of variation	df		EMS
Synthetics (S)	s-1	12	$\sigma^2 + 5\sigma^2_{SLY} + 10\sigma^2_{SL} + 10\sigma^2_{SY} + 20\sigma^2_{S}$
S x L	(s-1) (l- 1)	12	$\sigma^2 + 5\sigma^2_{SLY} + 10\sigma^2_{SL}$
S x Y	(s-1)(y-1)	12	$\sigma^2 + 5\sigma^2_{SLY} + 10\sigma^2_{SY}$
S x L x Y	(s-1)(l-1)(y-1)	12	$\sigma^2 + 5\sigma^2_{SLY}$
Error	ly (r-1)(s-1)	192	σ^2
Total	(lysr)-1	259	

RESULTS AND DISCUSSION

Weather conditions at the two locations during the two seasons of testing the synthetics were, in general, favorable. During the first season, however, heavy rains at Chitala caused severe waterlogging in the experimental plots, and a very strong wind at Chitedze caused considerable lodging, particularly in the CCA trial. These factors are reflected in the high coefficient of variation (CV) values for grain yield, 19.0% and 18.2% for CCC and CCA, respectively. The second season had even slightly higher CV values, 19.7% and 20.5% for CCC and CCA, respectively. This could be attributed to late planting of CCC at Chitala and more severe lodging in CCA. Population CCC was planted about two weeks after the onset of the rains and CCA had an overall lodged plants mean of 54.6% in the first season and 56.2% in the second season.

Performance of Synthetics

In the CCA population there were significant ($P \leq 0.01$) differences among synthetics over locations and years for the traits that were subjected to selection, but not for grain yield (Tables 5 and 6). This shows that selection was effective and that there was no significant correlated response for yield. Synthetic by location and synthetic by year interactions were significant for days to silking and grain index. The CV values for all three selected traits were relatively small, indicating the accuracy of the tests for these traits.

Table 5. Mean squares from the Population CCA analysis for grain yield, days to silking, plant height, and grain index.

Source of Variation	Df	Mean Square			
		Grain Yield	Days to Silking	Plant Height	Grain Index
Locations, L	1	38.08**	13686.56**	13875**	3.82**
Year, Y	1	1.49	116.45**	9548**	26.56**
L x Y	1	11.76**	171.23**	38703**	0.00
Synthetics, S	12	0.94	30.15**	1172**	7.28**
L x S	12	0.72	3.23*	181	0.22*
Y x S	12	0.99	8.19**	80	0.37**
L x Y x S	12	0.23	1.81	121	0.15
Rep (L x Y)	16	3.10**	5.40	1030**	0.21*
Error	192	0.88	2.00	146	0.11
Total	259				
CV (%)		19.0	2.2	3.9	11.6

*, **Significant at the 0.05 and 0.01 probability levels, respectively.

Table 6. Mean grain yields of 13 CCA synthetics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall
	1984/85	1985/86	Mean	1984/85	1985/86	Mean	Mean
	----------		Mgha^{-1}		----------		
Synthetic 1	5.1	4.2	4.6AB*	4.8	5.7	5.3A	4.9A
Synthetic 2	5.3	5.2	5.3A	5.1	5.6	5.4A	5.3A
Synthetic 3	4.8	4.7	4.8AB	5.0	5.8	5.4A	5.1A
Synthetic 4	4.8	3.6	4.2B	5.0	5.1	5.1A	4.6A
Synthetic 5	4.6	3.9	4.2B	5.3	5.1	5.2A	4.7A
Synthetic 6	4.2	4.5	4.3AB	4.7	5.9	5.3A	4.8A
Synthetic 7	4.6	4.8	4.7AB	5.1	5.6	5.3A	5.0A
Synthetic 8	3.9	4.4	4.1B	5.0	5.7	5.4A	4.7A
Synthetic 9	4.1	4.0	4.1B	4.9	5.6	5.3A	4.7A
Synthetic 10	5.2	4.3	4.7AB	4.9	4.6	4.8A	4.7A
Synthetic 11	4.4	4.6	4.5AB	4.6	5.6	5.1A	4.8A
Synthetic 12	4.6	4.1	4.3AB	4.8	5.4	5.1A	4.7A
CCA (Check)	4.0	3.7	3.9B	4.7	5.6	5.1A	4.5A
Mean	4.6	4.3		4.9	5.5		

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

The situation in the CCC population was similar to that observed in CCA in that significant differences ($P \leq 0.01$) were observed among synthetics for the traits that were subjected to selection (Table 7). However, unlike CCA, the CCC synthetics showed a significant ($P \leq 0.05$) correlated response for yield. The significant synthetics mean square for grain yield was caused largely by the higher yields of the tall, dent Synthetics 8 and 12 compared with the short, semiflint Synthetics 5 and 9 (Table 8). Synthetic by location interaction was significant for yield only, whereas synthetic by year interaction was significant for days to silking and plant height. The significant synthetic by location interaction for grain yield in CCC (Table 7) was caused to a large extent by low yields of Synthetics 2, 6, 9 and the check (CCC) at Chitedze relative to those at Chitala (Table 8). Coefficient of variation values for the traits subjected to selection were small as those observed in CCA.

The genotype by environment (G x E) interactions for days to silking were similar in both CCA and CCC synthetics in that the synthetic by year component was larger than that of synthetic by location (Tables 5 and 7). In fact, in CCC the latter was not significant. This emphasizes the importance of replication not only in terms of locations but also in terms of seasons. In the CCA synthetics at Chitedze in 1984/1985, Synthetics 7 and 10 silked earlier and Synthetic 4 silked later than expected according to the S_0 means (Table 9). At Chitala, Synthetic 5 silked later than expected in both seasons whereas Synthetics 10 and 6 silked later in the first and second seasons, respectively. In the CCC population, Synthetic 11 silked earlier and Synthetic 6 silked later than expected in the first and second seasons, respectively (Table 10). These

Table 7. Mean squares from the Population CCC analysis for grain yield, days to silking, plant height, and grain index.

Source of Variation	Df	Mean Square			
		Grain Yield	Days to Silking	Plant Height	Grain Index
Locations, L	1	2.60*	11039.67**	29027**	14.12**
Year, Y	1	9.93**	1842.85**	554*	11.22**
L x Y	1	48.07**	356.85**	21632**	0.54*
Synthetics, S	12	1.93*	44.81**	2996**	0.53**
L x S	12	1.58*	2.61	181	0.09
Y x S	12	1.30	5.75**	261*	0.18
L x Y x S	12	1.67*	2.06	129	0.13
Rep (L x Y)	16	1.50*	2.41	198	0.16
Error	192	0.93	2.12	146	0.14
Total	259				
CV (%)		19.4	2.1	5.0	11.3

*, **Significant at the 0.05 and 0.01 probability levels, respectively.

Table 8. Mean grain yields of 13 CCC syntehtics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall
	1984/85	1985/86	Mean	1984/85	1985/86	Mean	Mean
	----------	----------	Mgha^{-1}	----------	----------	----------	----------
Synthetic 1	5.5	4.7	5.1ABC*	5.2	5.4	5.3AB	5.2ABC
Synthetic 2	5.6	4.1	4.8ABCD	5.5	5.4	5.4A	5.1ABCD
Synthetic 3	5.7	4/5	5.1ABC	4.0	5.1	4.5BC	4.8BCDE
Synthetic 4	5.6	3.1	4.4BCD	4.4	5.3	4.9ABC	4.6CDE
Synthetic 5	5.0	4.6	4.8ABCD	3.4	5.1	4.3C	4.5DE
Synthetic 6	5.5	3.4	4.4BCD	4.4	6.0	5.2AB	4.8BCDE
Synthetic 7	6.0	4.5	5.3AB	4.8	5.5	5.1AB	5.2ABC
Synthetic 8	5.7	5.6	5.6A	5.5	5.1	5.3AB	5.5A
Synthetic 9	5.1	3.2	4.1D	4.9	4.9	4.9ABC	4.5E
Synthetic 10	5.3	4.6	4.9ABC	5.3	5.5	5.4A	5.2ABC
Synthetic 11	5.7	4.4	5.0ABC	5.9	4.8	5.4A	5.2ABC
Synthetic 12	5.7	5.4	5.6A	4.6	5.5	5.1AB	5.3AB
CCC (Check)	5.2	3.3	4.3CD	5.0	5.7	5.3A	4.8BCDE
Mean	5.5	4.3	4.8	5.3			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

Table 9. Mean days to silking of parental S_0 plants and of 13 CCA synthetics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall Mean	Means of S_0 Parents
	1984/85	1985/86	Mean	1984/85	1985/86	Mean		
	Days							
Synthetic 1	74.6	77.9	76.3D*	61.9	62.5	62.2GH	69.2D	70.5
Synthetic 2	74.7	78.9	76.8D	62.6	62.9	62.8FG	69.8D	71.6
Synthetic 3	73.9	78.4	76.2D	61.5	61.2	61.4H	68.8D	69.8
Synthetic 4	77.0	80.5	78.7BC	62.6	63.4	63.0EFG	70.9BC	70.7
Synthetic 5	75.5	79.0	77.3DC	63.4	65.0	64.2CD	70.7BC	70.9
Synthetic 6	78.4	80.5	79.4AB	64.2	62.5	63.3DEF	71.4B	70.7
Synthetic 7	75.6	81.0	78.3BC	63.4	63.5	63.5DEF	70.9BC	73.6
Synthetic 8	78.0	79.6	78.8B	64.2	64.0	64.1CD	71.5B	75.8
Synthetic 9	78.5	79.6	79.1AB	65.5	63.4	64.5BC	71.8B	74.9
Synthetic 10	76.6	81.6	79.1AB	64.8	65.7	65.2AB	72.2AB	75.6
Synthetic 11	78.4	79.4	78.9B	66.1	63.7	64.9BC	71.9B	74.9
Synthetic 12	79.7	81.0	80.3A	66.3	66.1	66.2A	73.3A	77.3
CCA (check)	78.0	79.9	78.9AB	64.5	63.5	64.CE	71.5B	--
Mean	76.8	79.8		63.9	63.7			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

Table 10. Mean days to silking of parental S_0 plants and of 13 CCC synthetics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall Mean	Means of S_0 Parents
	1984/85	1985/86	Mean	1984/85	1985/86	Mean		
	Days							
Synthetic 1	69.2	76.4	72.8F*	58.1	61.4	59.7FG	66.3H	64.9
Synthetic 2	68.9	76.5	72.7F	57.6	61.2	59.4G	66.1H	64.6
Synthetic 3	68.8	77.8	73.3F	60.3	61.9	61.1DE	67.2FG	64.9
Synthetic 4	68.5	77.4	73.0F	58.0	62.0	60.0FG	66.5GH	65.1
Synthetic 5	70.4	77.7	74.0DEF	60.6	61.9	61.3DE	67.6EF	68.4
Synthetic 6	70.8	79.3	75.1BCD	59.8	63.0	61.4CDE	68.2DE	68.5
Synthetic 7	71.5	81.1	76.3AB	60.3	63.9	62.1BCD	69.2BC	68.7
Synthetic 8	72.3	77.6	75.0BCD	61.3	64.1	62.7B	68.8CD	68.8
Synthetic 9	71.7	78.9	75.3BCD	61.5	63.8	62.6B	69.0C	71.4
Synthetic 10	72.7	80.0	76.4AB	60.6	64.2	62.4BC	69.4BC	72.0
Synthetic 11	72.5	81.6	77.1A	61.9	67.5	64.7A	70.9A	72.4
Synthetic 12	73.3	78.9	76.1ABC	63.2	64.7	64.0A	70.0AB	72.3
CCC (check)	71.1	78.2	74.6CDE	59.5	61.9	60.7EF	67.7EF	--
Mean	70.9	78.6		60.2	63.2			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

differences may be due, among other factors, to the different weather conditions between the two seasons. During the 1985/1986 seasons, there was much higher than normal rainfall at both locations, lasting a little longer than normal compared with the previous season.

Differences in the response of grain type in CCA at different locations were more pronounced among the flint synthetics than their dent counterparts (Table 11). In general, the flint synthetics were more flint at Chitala than they were at Chitedze. Probably the heat at Chitala had some effect on the development of the kernels, especially the loss of moisture as the kernel matured.

The effect of season on grain index was slightly different from the locational effect in the CCA synthetics (Table 11). There was a wider range in index values in the second season than in the first, which probably accounts for much of the synthetic by season interaction mean square.

Some of the CCC synthetics which were tall in the 1984/1985 season were significantly shorter in the 1985/1986 season, and vice versa (Table 12). The highest source of this synthetic by year interaction seems to be at Chitedze where Synthetics 9 and 11 and the check (CCC) were much taller in the 1984/1985 season.

In the CCC population, the best overall entry in grain yield was Synthetic 8, which significantly ($P \leq 0.05$) outyielded the check (CCC) by 14% (Table 8). At Chitedze the best entries were Synthetics 8 and 12, which outyielded the check by 30%. At Chitala none of the synthetics was superior to the check.

Table 11. Grain index means for parental S_0 plants and 13 CCA synthetics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall Mean	Means of S_0 Parents
	1984/85	1985/86	Mean	1984/85	1985/86	Mean		
	Days							
Synthetic 1	2.6	2.8	2.7EF*	2.1	2.2	2.2F	2.4F	1.0
Synthetic 2	2.6	3.4	3.0CD	2.8	3.3	3.1C	3.0CD	3.0
Synthetic 3	3.5	4.3	3.9AB	3.2	4.4	3.8B	3.9AB	5.0
Synthetic 4	2.3	2.8	2.5F	2.2	2.4	2.3EF	2.4F	1.0
Synthetic 5	2.9	3.4	3.1CD	2.7	3.1	2.9CD	3.0CD	3.0
Synthetic 6	3.6	4.2	3.9AB	3.2	4.4	3.8B	3.9AB	5.0
Synthetic 7	2.4	3.2	2.8DEF	2.2	2.8	2.5E	2.7EF	1.0
Synthetic 8	2.7	3.5	3.1CD	2.5	3.2	2.8D	3.0CD	3.0
Synthetic 9	3.5	4.7	4.1A	3.6	4.6	4.1A	4.1A	5.0
Synthetic 10	2.3	2.9	2.6F	2.0	2.3	2.1F	2.4F	1.0
Synthetic 11	2.9	3.3	3.1CD	2.2	2.7	2.4E	2.8D	3.0
Synthetic 12	3.6	3.9	3.8B	3.3	4.2	3.8B	3.8B	5.0
CCA (check)	2.9	3.8	3.3C	2.7	3.4	3.1C	3.2C	--
Mean	2.9	3.5		2.7	3.3			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

Table 12. Mean plant heights of parental S_0 plants and CCC synthetics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall	Means of
	1984/85	1985/86	Mean	1984/85	1985/86	Mean	Mean	S_0 Parents
	---------- Days ----------							
Synthetic 1	246.7	236.4	241.6G*	215.2	230.7	223.0F	232.3HI	235.3
Synthetic 2	251.0	233.8	242.4FG	215.1	240.1	227.6DEF	235.0GHI	241.0
Synthetic 3	261.8	247.9	254.9DEF	221.3	240.3	230.8DEF	242.8EF	264.8
Synthetic 4	277.3	256.7	267.0BCD	224.8	258.1	241.5BC	254.2CD	277.7
Synthetic 5	254.6	229.6	242.1G	205.6	221.4	213.5G	227.8I	241.0
Synthetic 6	257.5	226.9	242.0G	219.4	238.4	228.9DEF	235.5FGH	243.1
Synthetic 7	268.0	250.2	259.3CDE	223.3	248.0	235.7BCD	247.5DE	276.4
Synthetic 8	276.7	264.4	270.5ABC	239.2	249.3	244.3AB	257.4BC	282.6
Synthetic 9	263.2	231.1	247.2EFG	225.7	233.8	229.8DEF	238.5FGH	240.0
Synthetic 10	250.2	240.8	245.5FG	230.4	240.3	235.4CDE	240.4EFG	242.1
Synthetic 11	293.5	258.5	276.0AB	250.4	250.7	250.6A	263.3AB	289.8
Synthetic 12	290.0	269.9	280.0A	246.6	256.7	251.6A	265.8A	286.4
CCC (check)	261.5	230.0	245.8FG	222.7	231.2	226.9EF	236.3FGH	--
Mean	265.6	244.4		226.1	241.5			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

Response to Selection

In general, synthetics selected for earliness in silking tended to silk earlier than those selected for lateness in both CCA (Table 9) and CCC (Table 10). This trend compares favorably with the means of the selected parental S_0 plants. In CCA, Synthetics 1, 2, and 3 were significantly ($P \leq 0.05$) earlier than the check (Table 9). In CCC, Synthetics 1 and 2, both selected for earliness, were significantly ($P \leq 0.05$) earlier in silking than the check at each location and also over all environments (Table 10). The range in days to silking between the earliest and the latest synthetic was 4.8 for CCC and 4.5 for CCA synthetics, respectively, based on overall means.

Selection for plant height in both the CCA and the CCC populations was effective and the trend of the synthetics compared favorably with the parental S_0 means (Tables 12 and 13). In CCA, Synthetic 2, the shortest synthetic, was on the average 20.2 cm shorter than Synthetic 11, which was the tallest (Table 13). Synthetic 2, which also was the best yielder, measured 12.6 cm shorter than the check. This difference was significant ($P \leq 0.05$). In the CCC, the range in plant heights (Table 12) was 38 cm. Synthetic 5 was significantly ($P \leq 0.05$) shorter (8.5 cm) than the check.

The range in overall grain index was 2.4 to 4.1 (Table 11) for the CCA syntehtics and 2.7 to 4.1 (Table 14) for the CCC synthetics. The response to selection in both populations for this trait was remarkable, in view of the fact that selection was based on visual observation by two different crews.

Table 13. Mean plant heights of parental S_0 plants and CCA synthetics for two seasons at two locations.

Entry Parents	Chitedze 1984/85	Chitedze 1985/86	Chitedze Mean	Chitala 1984/85	Chitala 1985/86	Chitala Mean	Overall Means Mean	Means of S_0 Parents
	Days							
Synthetic 1	319.1	309.5	314.3CDE*	276.6	304.7	290.7EF	302.5CD	299.4
Synthetic 2	307.6	304.2	305.9E	274.6	313.7	294.2DEF	300.1D	305.0
Synthetic 3	320.5	308.5	314.5CDE	271.3	306.4	288.9F	301.7CD	306.5
Synthetic 4	325.1	310.3	317.7BCDE	292.3	328.1	310.2AB	313.9AB	338.5
Synthetic 5	331.3	314.4	322.9ABCD	297.7	326.1	311.9AB	317.4A	330.8
Synthetic 6	323.1	310.3	316.7BCDE	284.0	324.7	304.3BC	310.5ABCD	335.7
Synthetic 7	312.3	308.7	310.5DE	276.9	314.4	295.7DEF	303.1CD	303.5
Synthetic 8	305.6	305.3	305.4E	284.5	315.4	299.9CD	302.7CD	301.4
Synthetic 9	321.9	307.0	314.5CDE	278.2	317.3	297.8CDE	306.1BCD	300.2
Synthetic 10	336.3	318.9	327.6AB	293.8	328.2	311.0AB	319.3A	340.2
Synthetic 11	338.5	322.4	330.5A	284.2	336.0	310.1AB	320.3A	345.9
Synthetic 12	331.3	317.2	324.2ABC	297.4	332.5	315.0A	319.6A	338.0
CCA (check)	332.1	308.2	320.2ABCD	285.8	324.5	305.2BC	312.7ABC	--
Mean	323.4	311.1		284.4	320.9			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

In CCA, Synthetics 1, 4, and 10 were the best because they had the smallest grain index values, which is desirable. They were significnatly ($P \leq 0.05$) better than the check. In the CCC population, Synthetics 3, 5, and 7 had significantly ($P \leq 0.05$) smaller grain index values than the check.

In order to fully understand the response of one trait to selection and how it affected other traits, the sums of squares for the 12 selected synthetics were partitioned according to the original selection categories (early vs late; short vs tall; and flint, semi-flint, or dent). In both CCA and CCC, selection resulted in highly significant direct responses for all three traits (Tables 15 and 16). Differences between the contrasting groups were 1.8 and 3.3 in days to silking, 14.1 cm and 20.3 cm in plant height, and 1.4 and 1.0 in grain index for the CCA and CCC populations, respectively (Tables 17 and 18). Selection for days to silking in CCA had no effect on yield or grain index, but had a significant ($P \leq 0.01$) effect on plant height; in CCC, results were similar except that grain index also was affected ($P \leq 0.05$). Selection for plant height in CCA had a significant effect on days to silking and grain index at the $P \leq 0.01$ level, and on grain yield at the $P \leq 0.05$ level. In CCC, selection for plant height had a significant ($P \leq 0.01$) effect on days to silking but not on grain yield or grain index. Short synthetics tended to silk earlier and have a higher grain index (except for CCC) than tall synthetics. Selection for low and high grain index resulted in a difference ($P \leq 0.05$) of 0.5 in days to silking for CCA synthetics, and 0.2 in days to silking for CCC (which was not significant) between the

Table 14. Grain index means for parental S_0 plants and 13 CCC synthetics for two seasons at two locations.

Entry	Chitedze			Chitala			Overall	Means of S_0 Parents
	1984/85	1985/86	Mean	1984/85	1985/86	Mean	Mean	
	Days							
Synthetic 1	3.1	3.3	3.2EFG*	2.5	3.1	2.8C	3.0C	2.7
Synthetic 2	3.7	3.8	3.8CB	3.2	3.6	3.4B	3.6B	5.0
Synthetic 3	2.8	3.4	3.1FB	2.1	2.7	2.4D	2.7D	2.3
Synthetic 4	4.0	4.5	4.3A	3.6	4.1	3.8A	4.1A	5.0
Synthetic 5	2.7	3.2	3.0GH	2.0	2.7	2.4D	2.7D	2.6
Synthetic 6	3.5	4.3	3.9B	3.1	3.7	3.4B	3.7B	5.0
Synthetic 7	2.8	3.1	2.9GH	2.2	2.6	2.4D	2.7D	2.8
Synthetic 8	4.0	4.6	4.3A	3.4	3.9	3.6AB	4.0A	5.0
Synthetic 9	3.2	3.4	3.3EF	2.6	3.2	2.9C	3.1C	2.7
Synthetic 10	3.6	3.7	3.6CD	3.3	3.6	3.5B	3.5B	5.0
Synthetic 11	2.7	2.8	2.7H	2.2	2.3	2.3D	2.5D	2.3
Synthetic 12	3.9	3.9	3.9BC	2.9	4.0	3.4B	3.7B	5.0
CCC (check)	3.3	3.5	3.4DE	2.8	3.2	3.0C	3.2C	--
Mean	3.3	3.7		2.8	3.3			

*Means within locations in a column followed by different letters are significantly different at the 0.05 level.

Table 15. Mean squares resulting from partitioning the sums of squares for the 12 selected CCA synthetics according to the selection classes for each trait that was evaluated.

Trait selected	Df	Trait Evaluated			
		Grain Yield	Days to Silking	Plant Height	Grain Index
Early vs late	1	1.12	188.86**	1042.50**	0.00
Short vs tall	1	3.04*	117.46**	12027.50**	1.31**
Flint, semi-flint and dent	2	0.12	5.57*	8.04	41.96**
Error	176	0.88	2.00	144.46	0.11

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 16. Mean squares resulting from partitioning the sums of squares for the 12 selected CCC synthetics according to the selection classes for each trait that was evaluated.

		Trait evaluated			
Trait Selected	Df	Grain Yield	Days to Silking	Plant Height	Grain Index
Early vs late	2	0.24	223.54**	2918.48**	0.43*
Short vs tall	1	2.52	61.31**	24617.93**	0.00
Semi-flint vs dent	1	1.94	2.34	2188.29**	56.75**
Error	176	0.96	2.22	156.39	0.14

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 17. Means of CCA synthetics that were selected for contrasting maturity, height and grain index, and the CCA CO mean.

Selected classes	Trait Evaluated			
	Grain Yield ($Mgha^{-1}$)	Days to Silking	Plant Height (cm)	Grain Index
Early	4.9A*	70.1B	308B	3.1A
Late	4.8A	71.9A	312A	3.1A
Short	5.0A	70.3B	303B	3.2A
Tall	4.7B	71.7A	317A	3.0B
Flint	4.8A	70.8B	310A	2.5C
Semi-flint	4.9A	71.0AB	310A	2.9B
Dent	4.8A	71.3A	309A	3.9A
CO	4.5	71.5	313	3.2

*Means within traits in a column followed by different letters are significantly different at the 0.05 level.

Table 18. Means of CCC synthetics that were selected for contrasting maturity, height, and grain index, and the CCC CO mean.

Selected classes	Trait Evaluated			
	Grain Yield ($Mgha^{-1}$)	Days to Silking	Plant Height (cm)	Grain Index
Early	4.9A*	66.5C	241.1B	3.3A
Intermediate	5.0A	68.5B	242.1B	3.2B
Late	5.0A	69.8A	252.0A	3.2B
Short	4.9A	67.8B	234.9B	3.3A
Tall	5.1A	68.8A	255.2A	3.3A
Semi-flint	4.9A	68.4A	242.0B	2.8B
Dent	5.1A	68.2A	248.1A	3.8A
Co	4.8	67.7	236.3	3.2

*Means within traits in a column followed by different letters are significantly different at the 0.05 level.

Table 19. Selection differentials, gains, and realized heritabilities for maturity, plant height, and grain index in CCA and CCC.

Trait	Direction of Selection	Selection differential[+]		Gain[‡]		Realized h^2	
		CCA	CCC	CCA	CCC	CCA	CCC
Days to silking	Early	-2.9	-3.7	-1.4	-1.2	0.48	0.32
	Late	+2.9	+3.5	+0.4	+2.1	0.14	0.60
	Mean	--	--	--	--	0.31	0.46
Plant height (cm)	Short	-18	-20	-10	-1	0.56	0.05
	Tall	+18	+20	+4	+19	0.22	0.95
	Mean	--	--	--	--	0.39	0.50
Grain type	Flint	-2	-1.21	-0.7	-0.4	0.35	0.33
	Dent	+2	+1.22	+0.7	+0.6	0.35	0.49
	Mean	--	--	--	--	0.35	0.41

[+]Mean of selected S_0 parents minus overall S_0 mean.
[‡]Mean of synthetics minus mean of CO (CCA or CCC).
Gain divided by selection differential.

a significant effect on plant height in CCC but not in CCA (Tables 15, 16, 17 and 18). Selection for short plants in CCA, which is quite tall, resulted in a yield advantage of 11% over the check (CCA) (Table 17). In the shorter CCC population, the short-plant selections did not differ from the check (CCC) in yield (Table 18). The flint selections had a much smaller grain index than the checks, and the early synthetics were 1.4 and 1.2 days earlier than the checks in CCA and CCC, respectively.

Heritability Estimates from Regression

Regression coefficients were calculated as an estimate of heritability (h^2) of the traits selected for. Since the selected plants were mated among themselves to produce synthetics, one method of estimating heritability was by parent-offspring regression (synthetics on S_0 parents) (Falconer, 1960). Regression of S_1 lines on S_0 parents would be of limited value because of inbreeding depression in the S_1 lines. Realized heritabilities (h^2) were also calculated for each of the three traits by comparing the selection differential in the S_0 generation with the actual gains (difference between the CO population and selected synthetics). Heritability estimates by regression for CCA ranged from 32% for grain index to 37% for days to silking, and R^2 values ranged from 0.53 to 0.94 (Table 20). Realized heritability values ranged flints, which were earlier, and the dents. Selection for grain index had from 31% for days to silking to 39% for plant height (Table 19). In CCC, heritability estimates by regression ranged from 38% for grain index to 65% for plant height (Table 20), and realized heritabilities ranged from 41% for grain index to 50% for plant height. The two methods of calculating h^2 gave remarkably similar results. In CCA,

Table 20. Heritabilities (h^2) estimated by regression of means for days to silking, plant height, and grain index of CCA and CCC synthetics on means of S_0 parental plants.

Trait	CCA		CCC	
	$\overline{R^2}$	$\overline{h^2}$	$\overline{R^2}$	$\overline{h^2}$
Days to silking	0.53	0.37	0.85	0.47
Plant height	0.70	0.35	0.93	0.65
Grain index	0.94	0.32	0.82	0.38

means over the three traits were the same (35%) for the two methods. In CCC, the average over the three traits was 50% for the regression method and 46% for the realized h^2 method.

In CCA, the realized h^2 for early silking was larger (48%) than for late silking (14%); that for short height was also larger (56%) than for tall height (22%) (Table 19). This is probably because CCA had originally been selected for tall height and late maturity. Population CCC, on the other hand, had originally been selected for short plants and early maturity. In it, realized h^2 values were small for selection in the same direction (32 and 5% for early silking and shrot plants, respectively) in comparison with values for reverse selection (60 and 95%) (Table 19).

Correlation Among Traits

Correlations of practical importance (r greater than 0.5) were found between grain yield and plant height in CCC, plant height and days to silking in CCC, and lodging and days to silking in CCA (Table 21). A number of other combinations were correlated ($P \leq 0.01$), but the R^2 values were quite low. Higher grain yield and softer kernels were both associated with taller plants and later maturity. All the correlation coefficients were positive, indicating that selection for yield is likely to result in later maturity and taller plants. On the other hand, lodging can be reduced by selecting for shorter plants even though this might lead to lower yield. This means that a selection index should be used in which yield, height, maturity, and lodging are the main factors. All these should be considered in order to develop acceptable populations or hybrids.

Table 21. Phenotypic correlations among traits in CCA and CCC (n = 260).

Response of trait	Trait selected for	CCA		CCC	
		R^2	r	R^2	r
Grain yield	Grain index	0.011	0.104NS	0.049	0.222**
Grain yield	Plant height	0.087	0.295**	0.259	0.509**
Grain yield	Days to silking	0.231	0.481**	0.164	0.405**
Grain index	Plant height	0.038	0.195**	0.068	0.260**
Grain index	Days to silking	0.030	0.172**	0.115	0.340**
Plant height	Days to silking	0.092	0.303**	0.360	0.600**
Lodging (%)	Plant height	0.032	0.179**	0.002	0.045NS
Lodging (%)	Days to silking	0.452	0.672**	0.161	0.401**

SUMMARY AND CONCLUSIONS

A study was conducted to determine the response to selection of three traits, namely maturity, height, and endosperm type (flint vs dent), in two maize populations, CCA and CCC. Twelve synthetics in each population were developed on the basis of the three traits by intercrossing groups of selected S_1 lines. These synthetics were evaluated in two environments, one high altitude and cool (Chitedze) and one low altitude and hot (Chitala) for two seasons, 1984/1985 and 1985/1986.

There were significant ($P \leq 0.01$) differences among synthetics for the traits that were subjected to selection in both populations, indicating that selection was effective. The synthetic by year interaction was larger ($P \leq 0.01$) for days to silking than the synthetic by location interaction. This shows that variation between seasons was more important than variation between locations within any one season.

There was a highly significant direct response to selection for all three traits. Selection for plant height had a significant ($P \leq 0.01$) effect on days to silking and grain index but not on grain yield. Short synthetics tended to silk earlier and have a higher grain index than tall synthetics. Selection for grain index had no significant effect on plant height.

Heritability estimates by regression analysis and realized heritability values were in the 35 to 50% range, with good agreement

between the two methods. This indicates that good progress can be made by selection for any of the three traits, either by mass selection with control of both male and female parents or by intercrossing selfed progenies of selected plants.

There was no relationship between grain index and yield in CCA, but in CCC where there was a positive but small ($r = 0.22^{**}$) correlation between these traits. Yield was positively correlated with height and days to silking. There was a low but significant ($P \leq 0.01$) correlation between lodging and plant height in CCA but there was no correlation between these traits in CCC ($r = 0.045$). On the other hand, lodging was associated with later silking in both populations ($r = 0.67^{**}$ in CCA and 0.40^{**} in CCC).

These results indicate that it would be advisable to use index selection to improve the CCA and CCC populations for grain yield, lodging resistance, and flinty kernels, in order to minimize undesirable correlated responses.

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BIOGRAPHICAL SKETCH

Batson T. Zambezi was born on June 24, 1945, in Mulanje, Malawi. He graduated from Blantyre Secondary School in December 1965. The following year, he enrolled in the University of Malawi for a three-year period of study and obtained a Diploma in Agriculture in July 1969. He was employed by the Malawi Department of Agricultural Research as a technical officer in a maize-breeding program. In 1971, he attended a six-month course on maize breeding in New Delhi, India, organized by the FAO. In 1973, he joined the University of Malawi again for a Bachelor of Science degree in agriculture, which he obtained in July 1976. He went back to his technical officer position and was later appointed as maize breeder. In the fall of 1981, he joined the University of Florida for a Master of Science degree in agronomy, which he was awarded in December 1983. He then continued with his studies leading to the Doctor of Philosophy degree in agronomy.

Batson is married to Kalista and they have four children.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Earl S. Horner
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Daniel A. Roberts
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1987

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